HYBRIDIZATION, TAXONOMY AND AVIAN EVOLUTION

LESTER L. SHORT[1]

This report treats mainly the taxonomic significance of avian hybridization. I will take care of my impression of its evolutionary significance very briefly—(1) hybridization is insignificant in terms of hybrid origin of avian species, and (2) it is quite significant in terms of variation potential.

My approach to the investigation of hybridization is that of an evolutionary biologist, trained in taxonomy and with special interests in zoogeography, ethology, ecology, and genetics.

Birds offer various advantages for studies of hybridization and several disadvantages. Among the advantages are: (1) Birds are higher vertebrates whose primary senses, like ours, are visual and auditory. Sounds and sights are important to them, and they are employed behaviorally, including use as isolating mechanisms. Hence, we can appreciate the signals of birds more easily than signals used by most animals. (2) Birds are mainly diurnal, conspicuous and common. (3) Their geographic distribution is exceptionally well known. And (4) their systematics is relatively better known at the species level than that of other animals. Disadvantages are that: (1) Birds are difficult to maintain and are very difficult to breed in captivity in significant numbers. (2) They are hence rather poorly known genetically. And (3) they are highly mobile, that is they fly rapidly, they are very active, and often they are migratory. It might be noted also that their fossil record is poor, and hence we must largely base our knowledge of their relationships upon studies of modern birds.

My remarks deal mainly with hybridization in secondary contact and sympatric hybridization in nature. Following Anderson (1949), Stebbins (1959) and others, I include both intra- and interspecific hybridization, but bear in mind that all the interbreeding forms I shall mention are considered species by some ornithologists, even today.

Natural hybrids have been reported involving many avian species. I estimate that perhaps 40% of bird species ultimately will be shown to hybridize rarely to commonly. Our present knowledge of this phenomenon is uneven because of emphasis on game and other large species, on very distinctively marked species, and on species handled frequently by bird banders. Because many birds are sexually dimorphic, and males usually have brighter plumages than females, most reported hybrids are males, whereas less colorful female hybrids pass undetected. Many of the latter doubtless will be found eventually in present museum collections.

Only a few points will be noted here (see Short, 1969) concerning the significance of rare and unusual hybrids. Interspecific hybrids in this category can be evaluated taxonomically only after allowance is made for: (1) the

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[1] The American Museum of Natural History, New York, New York 10024.

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TABLE 1. Analysis of avian hybrid situations in North America.[a]

Situation	Number of Superspecies involved	Number of Species involved	Number of Cases[b] involved	Extent of Zone[c] Great	Extent of Zone[c] Small
Hybrid zones	—	16	19	10	9
Zones of overlap and hybridization	17	35	—	12	6
Hybrid swarms	3	5	4	0	4

[a] Data from Mayr and Short (1970); *only* the better documented cases are included (see text).
[b] Differs from "species involved" only intraspecifically for hybrid zones and hybrid swarms; a "case" is *one* pair of forms, and several different pairs of forms (subspecies or subspecies groups) may hybridize within a species, yielding several "cases."
[c] "Great" is 25 miles or more in extent (*not* width; see text), and "small" is less than 25 miles in extent.

relative opportunity for hybridization, that is the degree of actual sympatry within the group considered; and (2) the opportunity to recover hybrids. If there is much opportunity for interbreeding and for the recovery of hybrids within a particular group (*e.g.*, a family or a genus), then relative hybridization may provide useful taxonomic information.

Most hybrid birds are adults that often have undergone extensive migrations. The great number of avian hybrids (Gray, 1958) is puzzling in relation to the general view that animal hybrids encounter more severe homeostatic problems than do plant hybrids. The frequent survival to maturity in nature of hybrid birds, sometimes representing crosses between distantly related species, suggests that their physiology is not disrupted to the extent that has been thought. The occurrence of these hybrids indicates a great genetic similarity within many bird families. Crosses between species of different avian families are rare. Since an obvious correlation exists between the potential for hybridization and the degree of relationship, the occurrence and survival to adulthood of *any* hybrid, even in the aviary, is an indication of considerable genetic compatibility and resemblance.

More important are interspecific and intraspecific hybridization and backcrossing in secondary contacts (see Table 1). Among 517 extant species and superspecies of birds nesting in North America, 35 or 7% hybridize in this manner (Mayr & Short, 1970). Each of these 35 situations involves at least two (sometimes three) forms that have been considered separate species in the past and may be so considered by an extreme taxonomic "splitter" today. These cases denote a critical stage of speciation—the test of the degree of divergence of two populations. Although the number of species affected is not very great it is significant because: (1) The species involved are not rare, local species, but are common, widespread, hence biologically successful species; examples are the mallard ducks (*Anas* [*platyrhynchos*][2]), flickers (*Colaptes auratus*), house wrens (*Troglodytes aedon*), orioles (*Icterus galbula*), towhees (*Pipilo erythrophthalmus*), juncos (*Junco hyemalis*), and others. And (2) allowing an average life of say 1,000,000 years for species, it is evident

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[2] Brackets indicate superspecies; see Amadon (1966) and Mayr and Short (1970).

that hybridization could have played a role in the evolution of many or possibly even most avian species. This possibility is reinforced by the occurrence of limited sympatric hybridization in overlap zones involving 17 other species and superspecies (these include over 34 distinct forms). Thus, an additional 3% of North American species may have hybridized more extensively in the recent past. Furthermore, additional Nearctic species hybridize outside North America (Mayr & Short, 1970). It is probably safe to say that hybridization has been a significant factor in the recent evolution of at least 15% of the Nearctic avifauna.

I suspect that hybridizing species have been favored in the Pleistocene, that is, more rapidly speciating avian species may have suffered a greater rate of extinction than have those speciating more slowly. In this view hybridization is assigned an important role as a source of recombination under the rapidly shifting environmental conditions of the Pleistocene. Although radically different in its effects from glaciation, the impact of European civilization on North America may be likened to that of a new glacial period. Hybridizing avian species, survivors of the Pleistocene, not surprisingly seem to be doing well in man-modified environments.

I have endeavored (Short, 1969) to utilize field data in evaluating the taxonomic status of hybridizing forms. When two populations come into contact and interbreed to any extent, one of two situations commonly results. In one case a "hybrid zone" develops. This zone, however extensive, is inhabited by a population comprised entirely of hybrids (and diverse recombinants). Gene exchange is free, breeding is random, and the taxa are considered conspecific (they represent subspecies, often of different subspecies groups). Such a hybrid zone is interposed between the parental populations and effectively *both* connects *and* separates them. Thus, the parental forms are *not* sympatric. The distance across the zone from one to the other parental population, here called its width, of course is determined by natural selection. Its "actual" width is not determinable from field data, for its "apparent" width varies depending upon the nature and the number of characters used. Biochemical characters, for example, often extend the area of a hybrid zone previously determined by external morphological features. The depth or extent of the zone (perpendicular to its width) is determined by diverse factors such as topography and vegetation. An example of an extensive hybrid zone is shown in Figure 1 (see also Table 1).

A second type of situation is one in which there is overlap of the parental forms with hybridization occurring within the area of overlap which is termed a "zone of overlap and hybridization." Thus, the hybridizing forms, considered species (allospecies comprising a superspecies; see Amadon, 1966), are sympatric. One must ascertain that the parental phenotypes are sufficiently frequent and regular to insure that they are not extreme recombinants. I use the arbitrary value of 5% or more of *each* parental phenotype (or phenotypes), but in practice no problems occur because substantial numbers of both parental phenotypes (usually totaling some 30 to 90% or more of the population in the zone) are present in most reported cases. At each edge of the zone one parental

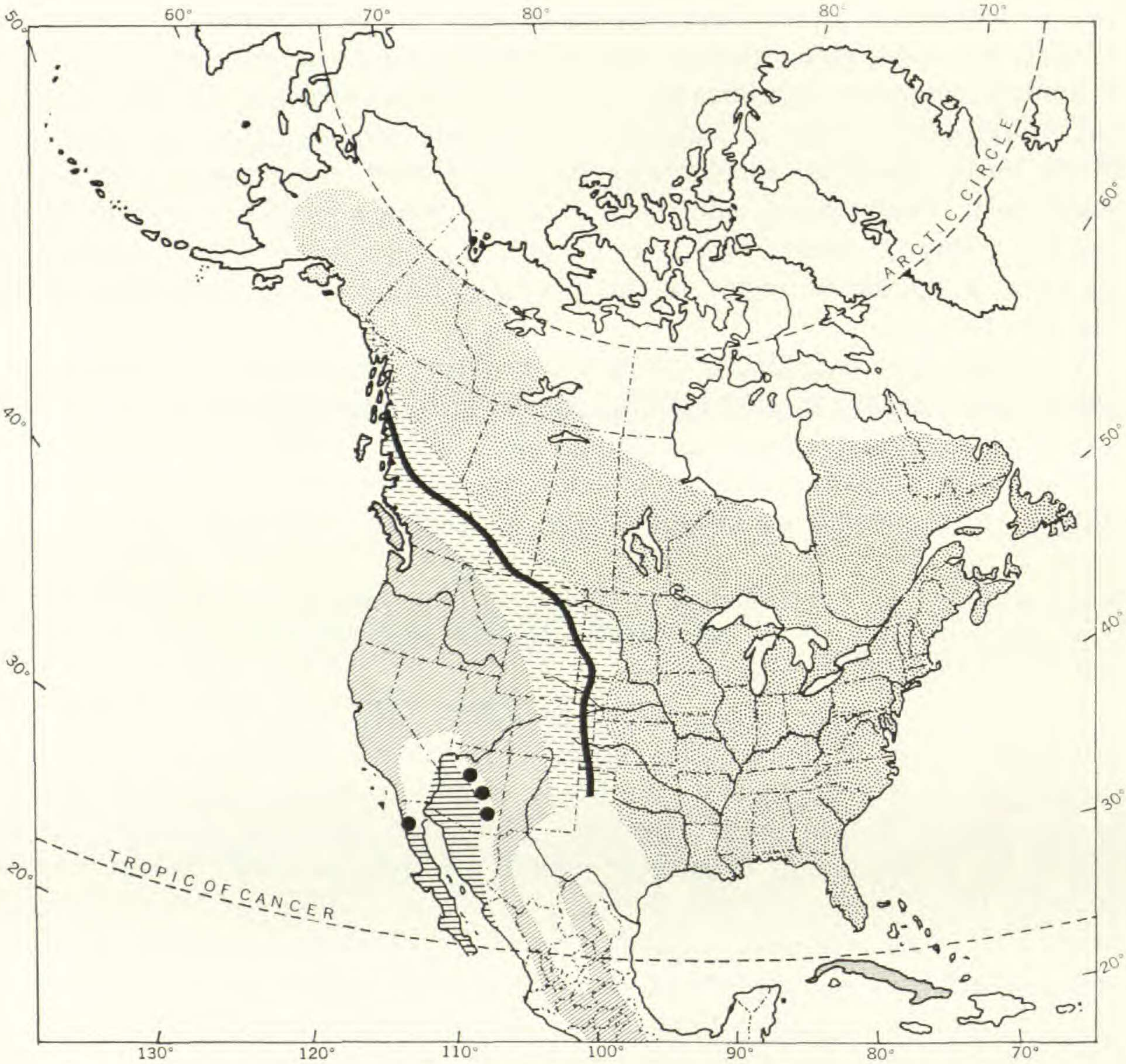

FIGURE 1. — The distribution of subspecies groups and hybrid zones in the North American flicker (*Colaptes auratus*). The groups are: *auratus* group—stippled; *chrysocaulosus* group—gray (Cuba); *cafer* group—diagonal lines; and *chrysoides* group—horizontal lines. A fifth group occurs allopatrically in highland Middle America. The *cafer* and *auratus* groups interbreed in an extensive hybrid zone, shown by dashed lines. The center of the hybrid zone is indicated by a heavy line. Note that the hybrid zone is broader to the west and south. Introgression affects populations of these groups as far as the West Coast and the East Coast, with stronger introgression (based on a 6-character analysis) to the west. Local hybridization in narrow (habitat-limited) hybrid zones and isolated hybrid swarms occur in the Southwest between the *cafer* and *chrysoides* groups, as shown by large black circles. (Adapted from map in Short (1965).)

species reaches the limit of its range and drops out, leaving the other species in allopatry. Figure 2 illustrates a zone of overlap and hybridization (see also Table 1).

Hybrid swarms are hybrid populations out of genetic contact with parental forms. While they present evidence that the parental forms are so closely related that hybrids and backcross products are viable (or even that recombinant genotypes can be selectively emphasized in the case of *stabilized* hybrid swarms), they do not permit full testing of the parental populations in

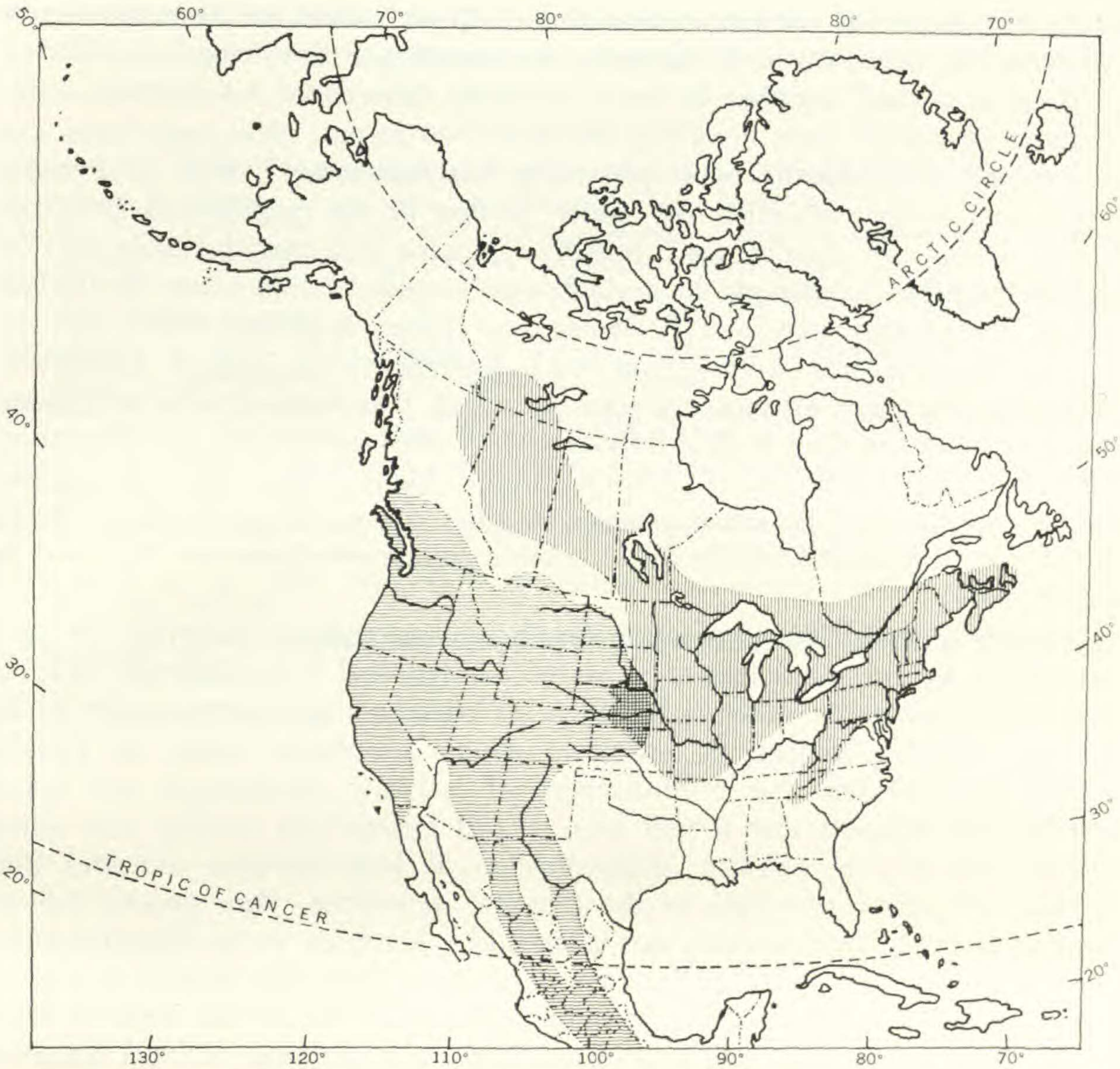

FIGURE 2. — The distribution of North American grosbeaks (*Pheucticus ludovicianus* superspecies) and their zone of overlap and hybridization. The eastern *P. ludovicianus* (vertical lines) meets and overlaps with western *P. melanocephalus* (horizontal lines) in the Great Plains. The zone of overlap and hybridization is shown by cross-hatching. Within this zone occur *both* parental species and numerous, diverse, hybrid phenotypes. Individuals of the parental species are about as numerous as are the hybrids in the center of the zone of overlap and hybridization. (Modified from map in West (1962) on the basis of studies by Short (unpublished).)

continuous contact. Rather their isolation renders local selection of paramount importance. I have previously (Short, 1969) discussed the taxonomic treatment of various types of hybrid swarms (see Table 1). Essentially I look to the situations involving the two forms elsewhere—that is, are they otherwise sympatric? Do adjacent populations show introgression? And, do other such swarms exist?—in order to render tentative decisions.

The various supposed and the few demonstrated cases of circular overlap, the famous "rings of races," are also discussed in Short (1969). If the intervening populations are connected by "true" hybrid zones and zones of primary intergradation, I considered the end forms to be conspecific despite their usually small area of overlap. Not more than five to 10 such cases are known in birds, and none has been shown conclusively to exemplify a true "ring."

There is a small number of cases involving differential interactions—combinations of various sorts involving the same two forms. Most such cases can be resolved taxonomically by emphasizing that interaction which is of major occurrence, or that affecting the major portion of the populations involved. At one extreme are cases in which broadly sympatric and reproductively isolated species hybridize extensively in a single area—some examples are the Indian bulbuls *Pycnonotus cafer* and *P. leucogenys* (Sibley & Short, 1959), and the Herring-Glaucous gulls (*Larus argentatus*, *L. hyperboreus*) in Iceland (Ingolfsson, 1970). At the other extreme are cases in which two forms interbreed wherever they meet, but the extent of hybridization varies—as between the *chrysoides* and *cafer* groups of the flicker *Colaptes auratus* (Short, 1965). The first extreme involves species, and the other extreme involves conspecific populations. Some of the very few, taxonomically difficult intermediate situations are discussed in Short (1969).

Finally, I would like to mention briefly several points concerning the persistence of hybrid zones and of zones of overlap and hybridization. Hybrids very much less viable either in the F_1 or in backcross generations ought to be strongly selected against. A recent computer simulation study by Crosby (1970) demonstrates that reinforcement of isolating mechanisms will occur rapidly, and suggests that it will even spread beyond the overlap area when hybrids are of low viability. Hybridization of long duration indicates that hybrids are about as viable as the parental genotypes. Any genetic factors tending to lessen their viability are balanced by heterosis, or by recombinations superior to parental genes in the zone of contact. That this should be true is suggested by the fact that the parental populations are at the limit of their ranges where they meet and hybridize. Under the pressure of local selection at their range limit, and often in tenuous genetic contact in but one direction with the main parental populations, it is not surprising that hybrids or some of their recombinants may be favored, perhaps strongly. This may retard or even halt the reinforcement of partly effective isolating mechanisms present when the secondary contact was formed. As a last point, there is evidence (citations are in Short, 1970) that many hybrid zones are ancient. Long-enduring hybrid zones suggest that hybrid genotypes are at a selective advantage within the zone, but that strong selection against at least some alien genes is occurring in the parental populations adjacent to the hybrid zone.[3]

In conclusion, the application of criteria based upon the biological species concept allows the taxonomic solution of most cases of avian hybridization. This serving of a taxonomic purpose, of course, is but a prelude to more detailed analyses, which may provide insight into the ecology, behavior, and genetics of such situations. As more data are obtained we can progress toward the eventual solution of such fundamental problems as the role of factors influencing

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[3] This action of natural selection differs in no way from that occurring adjacent to zones of primary intergradation between subspecies that have not been geographically isolated.

the *extent* of hybrid zones, and of introgression, and the functional relation to hybridization of morphological features, such as those used in hybrid indexes.

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